Biological Conservation 204 (2016) 181–188

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/bioc

Dead-wood addition promotes non-saproxylic epigeal arthropods but effects are mediated by canopy openness

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ARTICLE INFO

Article history:
Received 28 June 2016
Received in revised form 22 September 2016
Accepted 30 September 2016
Available online 15 October 2016

Keywords:
Araneae
Coleoptera
Collembola
Epigeic
Forest conservation
Woody debris

ABSTRACT

Restoring dead-wood amounts in forests is an increasingly and successfully applied conservation measure to counteract negative effects of intensive logging on biodiversity of saproxylic taxa. By contrast, if and how dead-wood addition benefits the vast number of non-saproxylic forest taxa, and how this varies with contextual factors like canopy openness, remains poorly understood. To enhance dead-wood addition strategies, it is thus important to understand how dead wood affects entire forests communities, not just saproxylic taxa. To untangle effects of dead-wood addition and canopy openness on non-saproxylic epigeal arthropods, we exposed different amounts of logs and branches on 190 0.1-ha plots located in sunny or shady mixed montane forests and sampled epigeal arthropods over three years. Canopy openness was a major driver of species assemblage composition and clearly mediated the effects of dead wood on epigeal beetles, spiders/harvestmen and springtails. Most species groups responded positively to the addition of dead wood. All groups decreased in number with increasing distance to dead wood. Dead wood affected taxa of both lower and higher trophic levels directly and taxa of higher trophic levels benefitted also indirectly owing to bottom-up effects. Our results indicate that increasing the amount of dead wood for conservation of saproxylic taxa benefits also non-saproxylic epigeal arthropods and thus, a larger number of forest species than commonly assumed. Because of the strong effects of canopy openness, similar to those found for saproxylic taxa, dead wood in both sunny and shady forest stands is needed.

1. Introduction

Dead wood is a keystone structure in forested ecosystems supporting a large fraction of forest biodiversity. An estimated 20–30% of all forest arthropod species are saproxylic, for example, meaning they are directly or indirectly dependent on dying or dead wood (Stokland et al., 2012). Intensive forestry practices result in drastic reductions in the amount and variety of dead wood compared to unmanaged forests (Lassauce et al., 2011, and references therein). Because of the loss of dead-wood habitats, many saproxylic taxa have declined and are now threatened (e.g., Nieto and Alexander, 2010). To counteract loss of saproxylic biodiversity, in many countries, particularly in Europe and North America, conservation strategies aim at increasing dead-wood volumes (e.g., Davies et al., 2007; Junninen and Komonen, 2011; Kilgo and Vukovich, 2014; Seibold et al., 2015). A worldwide meta-analysis has shown consistently positive effects of dead-wood addition on biodiversity of saproxylic taxa, but a very heterogeneous response of non-saproxylic taxa (Seibold et al., 2015). Saproxylic populations benefit directly from increased habitat availability (Lassauce et al., 2011; Müller and Bütler, 2010) due to an increase in habitat heterogeneity (Seibold et al., 2016), but mechanisms behind the effects of dead wood on non-saproxylic organisms remain poorly resolved.

Among non-saproxylic taxa, epigeal arthropods are a species-rich group with a highly variable response to increased amounts of dead

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http://dx.doi.org/10.1016/j.biocon.2016.09.031

wood (Seibold et al., 2015), possibly due to various direct and indirect mechanisms by which species of different trophic levels are linked to dead wood. Added dead wood, for instance, increases structural complexity on the forest floor by increasing surface area that differs qualitatively from the surrounding leaf litter but also by trapping and accumulating leaf litter (Castro and Wise, 2010; Kappes et al., 2009). Decaying woody debris provides nutrients that benefits detritivores like springtails (Collembola) or, owing to bottom-up effects, predators such as carabid beetles (Coleoptera) and spiders (Araneae) (Chen and Wise, 1999). Dead wood, particularly large logs, represents a relatively stable source of moisture that might be beneficial for many taxa that are sensitive to strong fluctuations in moisture, particularly under sunny conditions (Ulyshen et al., 2011). Furthermore, crevices in dead wood and accumulated litter can provide shelter from extreme temperatures (Langlands et al., 2011) and from predators (Hoddle, 2003). In turn, predators might be attracted by dead wood because of increased prey abundance (Klecka and Boukal, 2014). These effects could differ among species groups depending on the diameter of the dead wood and the tree species (Castro and Wise, 2010; Castro and Wise, 2009). Therefore, not only the amount of dead wood but also the number of different types of dead wood, i.e. dead-wood diversity (Siitonen et al., 2000), might affect epigeal arthropod assemblages.

When dead wood is created intentionally during logging or restoration operations or by natural disturbances, openings in the forest are generated ranging from downed single trees to large forest clearings and thus, result in increased insolation and altered microclimatic conditions. This leads to higher mineralization rates and promotes higher densities of herbs and grasses, which in turn can affect epigeal taxa, as shown by numerous studies focusing on effects of logging on epigeal arthropods (e.g., Gunnarsson et al., 2004; Johansson et al., 2016; Koivula and Niemelä, 2003; Nittérus and Gunnarsson, 2006). Canopy openness has the potential to interact with effects of dead wood on epigeal arthropods (Thorn et al., 2016). Dead wood in open areas, for instance, might play a more important role in buffering against microclimatic extremes than dead wood beneath a closed canopy. To our knowledge, only one study has aimed at decoupling the effects of canopy opening and dead-wood addition on epigeal arthropods. By experimentally mimicking hurricane disturbance, Richardson et al. (2010) revealed that effects of canopy opening on litter-dwelling arthropods were stronger than effects of leaf and branch deposition in a tropical forest in Puerto Rico. However, the understanding of the mechanisms of how dead wood affects epigeal arthropods and how these effects interact with canopy openness remains limited.

We aimed at an understanding of the direct and indirect effects of dead wood and canopy openness on non-saproxylic epigeal arthropod taxa of different trophic levels in temperate mixed forests. We experimentally added logs and branches on 190 plots to form gradients of dead-wood amount and dead-wood diversity. Half of these plots were located in sunny clearings and the other half were under a closed canopy. We sampled epigeal beetles, spiders, harvestmen and springtails on each plot during the early-successional phase at two distances from added dead wood. We tested the following hypotheses: i) epigeal arthropod abundance, richness and assemblage composition differ between sunny and shady forests; ii) the amount of dead wood per plot has direct positive effects on taxa of both lower and higher trophic levels and this pattern is stronger under sunny conditions than under shaded conditions; iii) the diversity of dead wood per plot positively affects species richness of taxa of both lower and higher trophic levels; iv) epigeal arthropod abundance and richness are higher when closer to dead wood and this pattern is stronger under sunny conditions than under shaded conditions; and v) taxa of higher trophic levels benefit from dead wood indirectly owing to increased densities of taxa of lower trophic levels (bottom-up effects).

2. Methods

2.1. Study area and experimental design

The experiment was conducted in the Bavarian Forest National Park in south eastern Germany. Overall, 190 0.1 ha plots were established in a randomized block design with five blocks across the management zone of the national park (Seibold et al., 2016; Seibold et al., 2014). Within each block, half of the plots (i.e. 19) were established in sunny clearings and the other half were established in mature forests under a closed canopy. Control plots had no dead wood. To the test plots, we added logs (diameter: 25–50 cm, length: 5 m) and/or branches (diameter: 3–5 cm, length: 2–3 m) that were cut less than eight weeks before. Each plot received dead wood either of European Beech *Fagus sylvatica* or Silver Fir *Abies alba* or of both tree species. These tree species are naturally dominant species in the montane zone of our study area. We varied the amount of added dead wood per plot by adding either a low or high amount of branches (8 branches, about 0.2 m^3 ha^{-1} or 80 branches, about 2 m^3 ha^{-1}) or a low or high amount of logs (4 logs, about 10 m^3 ha^{-1} or 40 logs, about 100 m^3 ha^{-1}) or a combination of logs and branches of low or high amounts. A gradient of dead-wood diversity was formed by varying the number of different dead-wood types per plot covering four levels: 0 – control plots; 1 – one of each of the four substrate types; 2 – either both diameter classes of the same tree species or only one diameter class of both tree species; 4 – all four dead-wood types. The surface area of all logs and branches was summed per plot to characterize precisely the amount of dead wood (Heilmann-Clausen and Christensen, 2004).

One of our objectives was to study the role of dead wood addition relative to sun exposure at plots with no and high tree canopy cover. Naturally downed trees in gaps provide long lasting sun exposed dead wood because considerable parts of the tree are located meters above ground. In our experiment, we tried to mimic this to some extent by placing half of the logs on top of other logs such that some were partly elevated and half of the logs had full soil contact. Due to differences in light availability, the herb layer (all vascular plants <1 m height; estimated on all plots in July 2012 (Londo, 1976)) differed strongly between sunny and shady plots (Fig. A1). Sunny plots were characterized by a dense herb layer of vascular plants and especially grasses, while most shady plots contained only single plant individuals in the herb layer and only rarely higher densities of low shrubs and young trees. In contrast to shady plots, sunny plots faced a fast succession and increasing cover of tall grasses, such as *Calamagrostis villosa*, and particularly young trees, mostly Silver Birch *Betula pendula*, Mountain-Ash *Sorbus aucuparia* and Norway Spruce *Picea abies*. To keep conditions of sun exposure constant over the whole study period and to avoid that added dead wood was covered by tall grasses leaning over logs and branches, the herb layer on each plot was trimmed once a year between late July and mid of August. By using brushcutters, all young trees and shrubs were trimmed to approx. 20 cm in height to keep the plots open. Furthermore, the herb layer, particularly tall grasses, was trimmed in the immediate surroundings of added dead wood and both pitfall traps. Thus, the herb layer in large portions of the 0.1-ha plots remained undisturbed, but dead wood and traps were not overgrown. Because of the low growth potential in the shady understory, only single young trees had to be trimmed occasionally at shady plots.

2.2. Arthropod sampling and data processing

Epigeal arthropods were sampled using two pitfall traps per plot that were placed 5 m apart at a distance of 30 and 150 cm to the dead wood. Each trap consisted of a 400 ml polypropylene cup (95 mm diameter) sunk flush with ground level with a PVC roof placed over it about 5 cm above ground level to shield the trap from rain. A non-attracting 3% copper sulphate solution was used to kill and preserve trapped